Matrix Population Models for Wildlife Conservation and Management

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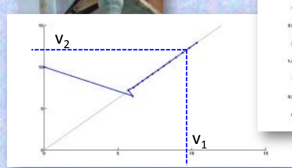
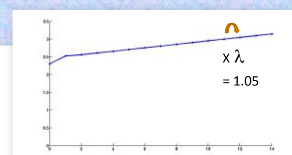
Lecture 3
Matrix model theory

Hal CASWELL, showing a matrix model to a Laysan Albatross.

Hal's book (Matrix models, Sinauer, 2001) can be used both as a textbook and as a comprehensive reference.

From numerical to formal results





$V = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$

$M\,V = \lambda\,V$

$M^t\,N_0 \rightarrow \alpha(N_0)\,\lambda^t\,V$
asymptotically

... in loose notation

From numerical to formal results

$$\begin{array}{lccccc} t = & 1 & 2 & 3 & \ldots\ 10 & 11 \\ M^t = & \begin{pmatrix} 0.3000 & 0.6000 \\ 0.5000 & 0.6500 \end{pmatrix} & \begin{pmatrix} 0.3900 & 0.5700 \\ 0.4750 & 0.7225 \end{pmatrix} & \begin{pmatrix} 0.4020 & 0.6045 \\ 0.5038 & 0.7546 \end{pmatrix} & \ldots \begin{pmatrix} 0.5666 & 0.8499 \\ 0.7082 & 1.0623 \end{pmatrix} & \begin{pmatrix} 0.5949 & 0.8924 \\ 0.7436 & 1.1154 \end{pmatrix} \\ M^t./M^{t-1} = & & \begin{pmatrix} 1.3000 & 0.9500 \\ 0.9500 & 1.1115 \end{pmatrix} & \begin{pmatrix} 1.0308 & 1.0605 \\ 1.0605 & 1.0445 \end{pmatrix} & \ldots \begin{pmatrix} 1.0500 & 1.0500 \\ 1.0500 & 1.0500 \end{pmatrix} & \begin{pmatrix} 1.0500 & 1.0500 \\ 1.0500 & 1.0500 \end{pmatrix} \end{array}$$

Termwise division

From numerical to formal results

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Termwise division

$M^t = M\,M^{t-1} \approx \lambda\,M^{t-1}$, similar to $M\,V = \lambda\,V$

$\Rightarrow M^{t-1}$ (and M^t) have columns $\approx$ proportional to V

$M^t \rightarrow \lambda^t \begin{pmatrix} u_1 V & u_2 V \end{pmatrix} = \lambda^t\,V U'$ with $U' = \begin{pmatrix} u_1 & u_2 \end{pmatrix}$

... in loose notation   transpose

Transposition and matrix product

the transpose of $U = \begin{pmatrix} u_1 \\ u_2 \end{pmatrix}$ is $U' = \begin{pmatrix} u_1 & u_2 \end{pmatrix}$

if $V = \begin{pmatrix} v_1 \\ v_2 \end{pmatrix}$, $V\,U' = \begin{pmatrix} v_1 u_1 & v_1 u_2 \\ v_2 u_1 & v_2 u_2 \end{pmatrix}$ is a 2 x 2 matrix

while $U'V = \begin{pmatrix} v_1 u_1 + v_2 u_2 \end{pmatrix}$ is a 1 x 1 matrix, i.e. a scalar,
also denoted as $\Sigma\, u_i v_i$

From numerical to formal results

$M^t \rightarrow \lambda^t \begin{pmatrix} u_1 V & u_2 V \end{pmatrix} = \lambda^t V U'$

Or, equivalently and more rigorously

$\lambda^{-t} M^t \rightarrow V U'$

$u_i > 0, v_i > 0$

$\lambda^{-(t+1)} M^{t+1} = \lambda^{-1} M \lambda^{-t} M^t \rightarrow \lambda^{-1} M V U' = V U'$

$= \lambda^{-t} M^t \lambda^{-1} M \rightarrow V U' \lambda^{-1} M$

Hence $V U' \lambda^{-1} M = V U'$

Premutiply by U' and simplify by scalar U'V, to get:

$U' M = \lambda U'$

Of eigenvalues and eigenvectors

Demographic ergodicity

$M V = \lambda V$ eigenvalue and right eigenvector

$U' M = \lambda U'$ eigenvalue and left eigenvector

$\lambda^{-t} M^t \rightarrow V U'$ leads to

$M^t N_0 \rightarrow \lambda^t V (U' N_0)$ asymptotic exponential growth

Scalar, weighting the components of N_0 by the u_i = « reproductive values »

Of eigenvalues and eigenvectors

Demographic ergodicity

λ, U, V are dispositional properties

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Of eigenvalues and eigenvectors

Usually, no formulas, but easy to get numerically

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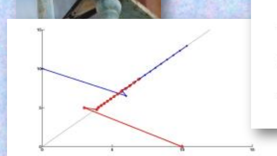
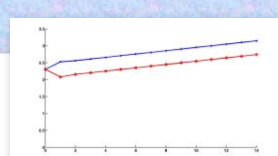
Reproductive values





lue and right eigenvector

eigenvalue and left eigenvector

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$M^t N_0 \rightarrow \lambda^t V (U' N_0)$ asymptotic exponential growth

Scalar, weighting the components of N_0 by the u_i = « reproductive values »

Why is it so?

These results do not hold for all matrices

M is such that M^t, for t large enough, has all its terms >0

... because M is a primitive, non negative, irreducible matrix

(a sufficient condition, not a necessary one)

Why is it so?

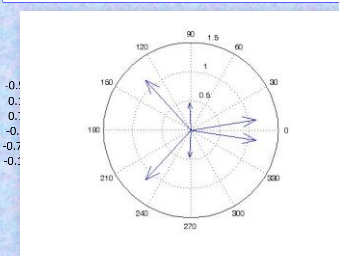
n x n Matrices have (in general) n eigenvalues which are complex numbers

$$M = \begin{pmatrix} -0.6579 & -0.0961 & -0.5214 & -0.3996 & -0.7195 & -0.1503 \\ 0.8771 & 0.6794 & 0.1578 & -0.1972 & -0.4797 & -0.7616 \\ 0.1810 & 0.0652 & 0.7338 & 0.6667 & -0.8264 & -0.0099 \\ -0.1187 & 0.1078 & -0.1864 & -0.1927 & -0.1412 & 0.4128 \\ 0.8838 & 0.3601 & -0.7748 & -0.2196 & -0.4854 & -0.5129 \\ 0.3118 & -0.2656 & -0.1123 & -0.2791 & -0.4049 & 0.5701 \end{pmatrix}$$

Why is it so?

n x n Matrices have (in general) n eigenvalues which are complex numbers

$$M = \begin{pmatrix} -0.6579 & -0.0961 & -0.5 \\ 0.8771 & 0.6794 & 0.1 \\ 0.1810 & 0.0652 & 0.7 \\ -0.1187 & 0.1078 & -0. \\ 0.8838 & 0.3601 & -0.7 \\ 0.3118 & -0.2656 & -0.1 \end{pmatrix}$$



Why is it so?

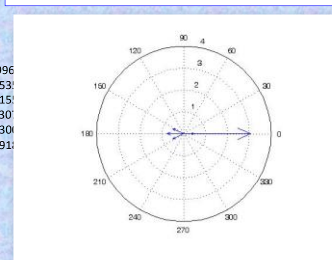
However, positive, nonnegative irreducible matrices …

$$M = \begin{pmatrix} 0.0842 & 0.0954 & 0.9969 & 0.0710 & 0.6135 & 0.8979 \\ 0.1639 & 0.1465 & 0.5535 & 0.8877 & 0.8186 & 0.5934 \\ 0.3242 & 0.6311 & 0.5155 & 0.0646 & 0.8862 & 0.5038 \\ 0.3017 & 0.8593 & 0.3307 & 0.4362 & 0.9311 & 0.6128 \\ 0.0117 & 0.9742 & 0.4300 & 0.8266 & 0.1908 & 0.8194 \\ 0.5399 & 0.5708 & 0.4918 & 0.3945 & 0.2586 & 0.5319 \end{pmatrix}$$

Why is it so?

However, positive, nonnegative irreducible matrices have their largest modulus eigenvalue which is a positive real number

$$M = \begin{pmatrix} 0.0842 & 0.0954 & 0.996 \\ 0.1639 & 0.1465 & 0.553 \\ 0.3242 & 0.6311 & 0.515 \\ 0.3017 & 0.8593 & 0.330 \\ 0.0117 & 0.9742 & 0.430 \\ 0.5399 & 0.5708 & 0.491 \end{pmatrix}$$



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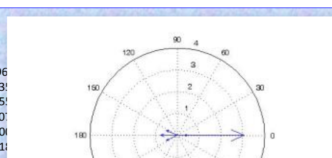


In products such as M^t, this "dominant eigenvalue" tends to outweigh the influence of other eigenvalues.

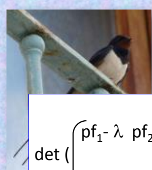
i.e., when $t \to \infty$ $M^t N(0) \to \alpha(0)\lambda^t V$

Of eigenvalues and eigenvectors

Usually, no formulas, but easy to get numerically

Eigenvalues are the roots of $\det\left(M - \lambda \begin{pmatrix} 1 & 0 & \dots & 0 & 0 \\ 0 & 1 & \dots & 0 & 0 \\ & & \dots & & \\ 0 & 0 & \dots & 1 & 0 \\ 0 & 0 & \dots & 0 & 1 \end{pmatrix}\right) = 0$

General Numerical Analysis software (Matlab, Mathematica…) or specialized software (ULM…) will get eigenvalues and eigenvectors for you.



Of eigenvalues and eigenvectors

The largest root of

$$\det \begin{pmatrix} pf_1 - \lambda & pf_2 \\ q_1 & q_2 - \lambda \end{pmatrix} = \lambda^2 - (pf_1+q_2)\,\lambda + pf_1\, q_2 - pf_2\, q_1 = 0$$

is

$$\frac{pf_1 + q_2 + \sqrt{(pf_1+q_2)^2 - 4\,(pf_1\, q_2 - pf_2\, q_1)}}{2}$$

Of eigenvalues and eigenvectors

Even when there is a formula, λ is not a linear or simple function of the parameters

$$\frac{pf_1 + q_2 + \sqrt{(pf_1+q_2)^2 - 4\,(pf_1\, q_2 - pf_2\, q_1)}}{2}$$

Of eigenvalues and eigenvectors

Even when there is a formula, λ is not a linear or simple function of the parameters

$$\frac{pf_1 + q_2 + \sqrt{(pf_1+q_2)^2 - 4\,(pf_1\, q_2 - pf_2\, q_1)}}{2}$$

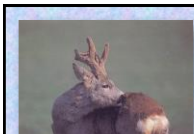
Yet, we need to know how λ varies when one or several parameter values change

Sensitivity analysis

What if swallows were not nesting at age 1 ?

$$M = \begin{pmatrix} 0.30 & 0.60 \\ 0.50 & 0.65 \end{pmatrix} \Rightarrow \lambda = 1.05$$

$$M = \begin{pmatrix} 0 & 0.60 \\ 0.50 & 0.65 \end{pmatrix} \Rightarrow \lambda = 0.9619$$



Sensitivity analysis What if ?

What if we harvest a proportion h of a population?

$M \rightarrow M_h = (1-h)M \qquad MV=\lambda V \Rightarrow (1-h)MV=(1-h)\lambda V$

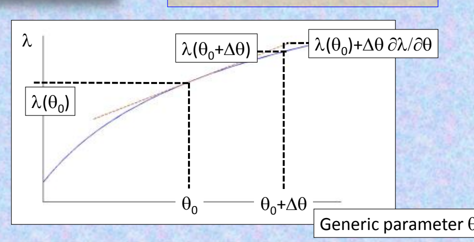
Hence $M_h V = (1-h)\lambda V$

$\lambda \rightarrow \lambda_h = (1-h)\lambda$, asymptotic structure V unchanged

If you harvest each year 30 % of a roe deer population whose growth rate is 40 % (λ=1.4), λ_h is 1.4*(1-0.3) = 0.98, i.e. the population will drop at a rate of 2 % per year

Sensitivity Analysis

In more general cases, λ can be approximated by a linear function



Sensitivity Analysis

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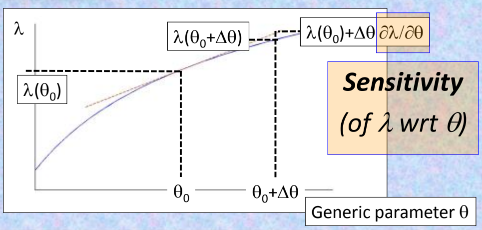


Sensitivity
(of λ wrt θ)

Sensitivity and Elasticity

Sensitivity $\partial\lambda / \partial\theta$
Absolute change in λ vs
Absolute change in θ

Elasticity

$\partial \text{ Log } \lambda / \partial \text{ Log } \theta = (\theta / \lambda)\, \partial\lambda / \partial\theta = (\partial\lambda / \lambda) / (\partial\theta / \theta)$

Relative change in λ vs relative change in θ

Matrix element $\theta = m_{ij}$
Lower-level parameter e.g. $\theta = f_1$ or $\theta = s_1$

Sensitivity to matrix element: perturbation analysis

$\partial\lambda / \partial m_{ij}$?

M V $= \lambda$ V [1] (M+dM)(V+dV) = (λ+dλ) (V+dV) [2]

M V + dM V + MdV + dM dV = λV + dλ V + λ dV + dλ dV [2']

M V + dM V + MdV + ~~dM dV~~ = λV + dλ V + λ dV + ~~dλ dV~~

From [1]: ~~M V~~ + dM V + MdV = ~~λV~~ + dλ V + λ dV [2'']

U' x [2'']: U'dM V + U'MdV = U'dλ V + λ U'dV

U'M=λ U': U'dM V = U'dλ V i.e. U'dM V = dλ U'V [3]

Sensitivity to matrix element: perturbation analysis

for a change in a single matrix term
$m_{ij} \rightarrow m_{ij}+dm_{ij}$,

$$dM = \begin{pmatrix} 0 & 0 & \cdots & & 0 \\ 0 & \cdots & dm_{ij} & \cdots & 0 \\ & & \vdots & & \\ 0 & 0 & \vdots & & 0 \end{pmatrix}$$

hence U'dM V $= u_i\, v_j\, dm_{ij}$ [4]

Sensitivity to matrix element: perturbation analysis

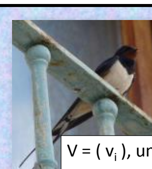
$\partial\lambda / \partial m_{ij}$?

U'dM V = dλ U'V [3]
U'dM V $= u_i\, v_j\, dm_{ij}$ [4]

$\partial\lambda / \partial m_{ij} = u_i\, v_j / \text{U'V} = u_i\, v_j / \Sigma\, u_i\, v_i$

a beautiful result due to Hal Caswell (1978)

$\partial\text{Log}\lambda / \partial \text{ Log } m_{ij} = u_i\, v_j / \text{U'V} = m_{ij}\, u_i\, v_j / \lambda\, \Sigma\, u_i\, v_i$



Sensitivity to matrix element: perturbation analysis

V = (v_i), under $\Sigma\, v_i = 1$, is the stable structure

$m_{ij}\, u_i\, v_j / \lambda$, under $\Sigma\, u_i\, v_i = 1$, is the *relative* contribution, *in asymptotic regime*, of component *i* to component *j*, *expressed with reproductive value as the currency.*

As a consequence, elasticities (wrt the m_{ij}) sum up to 1

Normalization used in general obvious from the context.
When speaking of sensitivity, we will often use $\Sigma\, u_i\, v_i = 1$

Then, $\partial\lambda / \partial m_{ij} = u_i\, v_j$

Sensitivity to lower-level par. the chain rule

$\partial\lambda / \partial\theta$?

$\partial\lambda / \partial\theta = \Sigma_i \Sigma_j (\partial\lambda / \partial m_{ij} \times \partial m_{ij} / \partial\theta)$

Barn Swallow example:

$\partial\lambda / \partial s_0 = \partial\lambda / \partial m_{11} \times \partial m_{11} / \partial s_0 + \partial\lambda / \partial m_{12} \times \partial m_{12} / \partial s_0$

$= u_1 v_1 f_1 + u_1 v_2 f_2$

$s_0 \partial\lambda / \partial s_0 = u_1 (v_1 f_1 s_0 + v_2 f_2 s_0)$

$MV = \lambda V \Rightarrow v_1 f_1 s_0 + v_2 f_2 s_0 = \lambda v_1$,

hence the elasticity of λ wrt s_0 :

$$s_0/\lambda \times \partial\lambda / \partial s_0 = u_1 v_1$$